

THE INTERPRETATION OF THE LOWER CRETACEOUS HETEROMORPH AMMONITE GENERA *PARACRIOCERAS* AND *HOPLOCRIOCERAS* SPATH, 1924

by P. F. RAWSON

ABSTRACT. *Ammonites (Crioceras) occultum* Seeley and *Hamites phillipsi* Phillips, the type species of *Paracrioceras* and *Hoplocrioceras* Spath, 1924, are redescribed and the original concept of the genera is reviewed. The 'Tethyan' forms *Emeriticeras* and *Aspinoceras* are regarded as junior subjective synonyms of *Paracrioceras* and *Hoplocrioceras* respectively. As defined by Spath, *Hoplocrioceras* embraces small forms with weakly aspinoceratid coiling together with larger, crioceratitid species; this definition cuts completely across existing generic classification of related Tethyan forms. The significance of shell coiling in the classification of some Lower Cretaceous heteromorphs is discussed briefly, and it is suggested that forms with aspinoceratid/ancyloceratid coiling may be dimorphs of larger, crioceratitid forms.

THE Lower Cretaceous heteromorphs *Ammonites (Crioceras) occultum* Seeley (1865) from the Snettisham Clay (Norfolk) and *Hamites phillipsi* Phillips (1829) from the Speeton Clay (Yorkshire) were designated type species of Spath's (1924) new genera *Paracrioceras* and *Hoplocrioceras* respectively. The generic names have subsequently been applied to a variety of late Hauterivian and Barremian species in north-west Europe, and occasionally further afield, but ignored by most recent workers on the Tethyan, especially French, faunas. Hence an impression is gained that both genera have a 'boreal' distribution when, in fact, their type species are remarkably close to some 'Tethyan' forms. However, the type species are poorly known since both were based on single, incomplete specimens and neither has been revised, though the holotype of *Hoplocrioceras phillipsi* has been described and refigured (Howarth 1962). A limited number of additional specimens allows the ontogeny of both to be outlined for the first time. Spath's (1924) concept of the genera is reviewed in the light of these descriptions.

DESCRIPTION OF THE TYPE SPECIES

Superfamily ANCYLOCERATACEAE Meek, 1876

Family ANCYLOCERATIDAE Meek, 1876

Subfamily CRIOCERATITINAE Wright, 1952

Genus PARACRIOCERAS Spath, 1924

Paracrioceras occultum (Seeley)

Plate 43, figs. 1-6; text-fig. 1a-b

v* 1865 *Ammonites (Crioceras) occultus* Seeley, p. 246, pl. 10, fig. 1.

v 1924 *Paracrioceras occultum* (Seeley); Spath, p. 79.

Holotype. Cookson Collection, Sedgwick Museum, Cambridge, B. 11129.

Type locality. 'Near Hunstanton' (Seeley 1865, p. 246). The specimen bears a later label claiming, possibly erroneously, that it is from the Heacham Brick Pit, near Snettisham.

Horizon. Snettisham Clay (mid Barremian). The holotype may have been obtained from the local boulder clay (Pleistocene), according to Seeley.

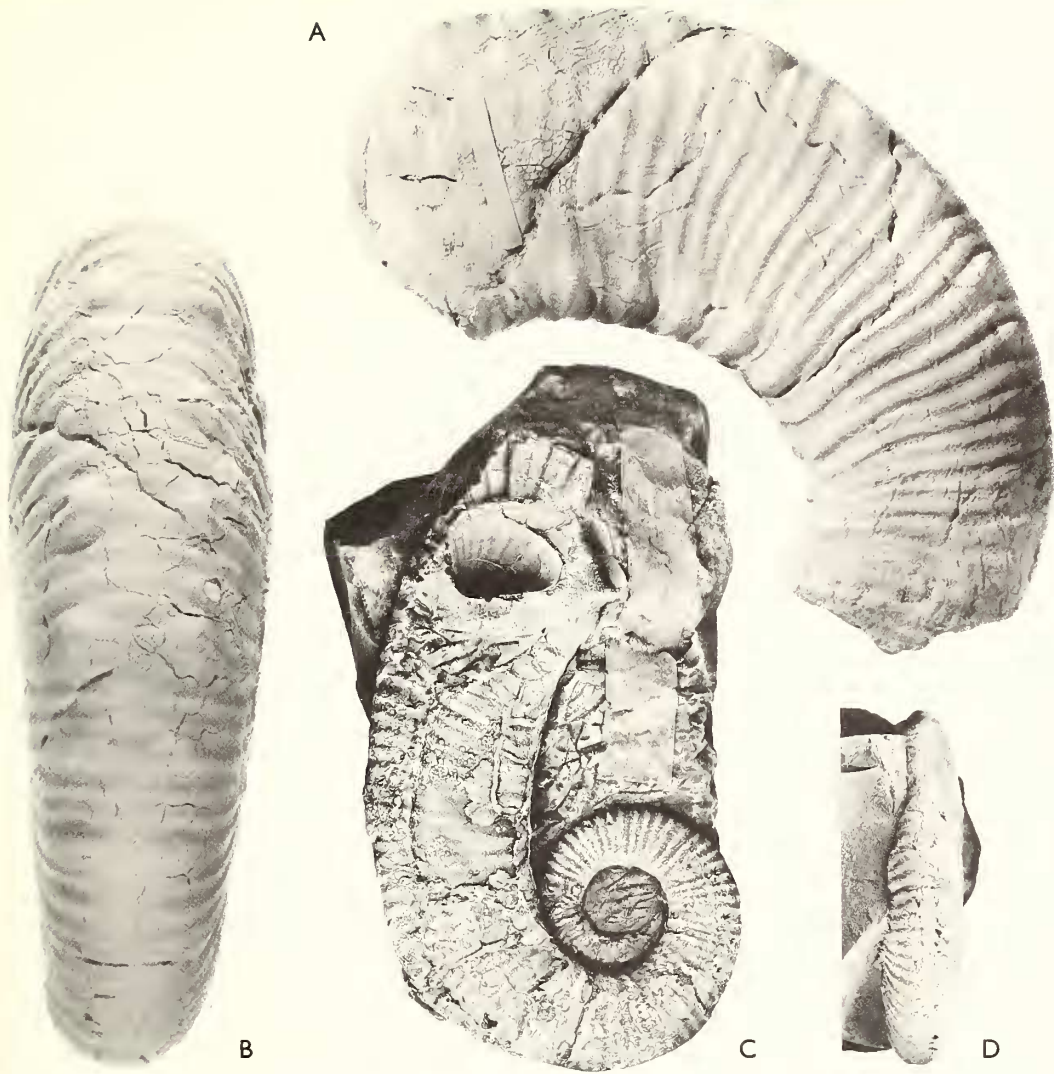
Other described material. Two specimens: Sedgwick Museum B. 11131 and B. 11797, from the Snettisham Clay at Heacham Brick Pit, near Snettisham.

Description. Although the holotype (text-fig. 1a-b) is a body chamber only, the other two specimens show earlier growth-stages; one (B. 11797) is a well-preserved body chamber and adjacent fragment of phragmocone, closely matching the holotype but with a crushed impression of earlier whorls, while the other (B. 11131) is a smaller individual of 86.5 mm diameter. Both were apparently examined by Spath during the preparation of his 1924 paper.

Coiling is regularly crioceratitid throughout; the first solidly preserved whorl starts at about 40 mm diameter (B. 11131) but rubber casts have been made from external moulds of earlier growth stages (B. 11131, B. 11797). These show that trituberculate ribs have already developed by about 12 mm diameter (B. 11797). From about 15 mm to about 70 mm diameter these ribs are swollen and bear long, sharp umbilical, mid-lateral, and ventro-lateral spines (bluntly rounded on internal moulds). The ventro-lateral spines touch the dorsum of the succeeding whorl. Between each trituberculate rib there are normally two or three (up to five in the early whorls of B. 11797) finer ribs which arise at the umbilical edge and remain non-tuberculate, or bear a small mid-lateral or ventro-lateral tubercle. Occasionally, the posterior rib of a group is associated with the preceding trituberculate rib, looping from the umbilical to mid-lateral tubercle of this stronger rib, then from the mid-lateral or ventro-lateral tubercle, and finally across the venter to the opposing ventro-lateral tubercle. Above about 70 mm diameter the strength of the trituberculate rib gradually diminishes, the mid-lateral tubercle reduces, and the whorl flank consequently becomes flatter (B. 11131, B. 11797), so that by about 85 mm diameter the ribs are almost equal in strength and mid-lateral tubercles have disappeared. This final, presumably adult, growth stage is well seen on both the body chamber of B. 11797 and the holotype (B. 11129).

Changes in the whorl section accompany the changes in sculpture. In the inner whorls the section is rounded, slightly higher than wide, and angular at umbilical and ventro-lateral edges. Sections across the trituberculate ribs are distinctly hexagonal. As the tuberculation diminishes, the whorl flanks flatten and height correspondingly increases, so that the whorl section of the holotype and body chamber of B. 11797 is subquadrate, the flanks almost flat but converging slightly towards the ventral region. The ventro-lateral shoulder and dorsal edge are angular. The dorsum is concave and crossed by forwardly curving rib-folds and finer growth lines. It bears an impression of the tip of the ventro-lateral tubercles of the preceding whorl, and slight indentations on the holotype apparently correspond with the ventro-lateral angle of the preceding whorl. These are absent on specimen B. 11797 and it is unlikely that the body chamber of the holotype was in contact with the penultimate whorl.

The flanks of the holotype are crossed by slightly flexuous ribs, some of which arise singly or in pairs from a radial umbilical swelling while others are intercalated at the angular umbilical edge or higher on the whorl flank. Prominent ventro-lateral



TEXT-FIG. 1. Holotypes. *a, b*, *Paracrioceras occultum* (Seeley), Sedgwick Museum B. 11129 (Cookson Collection), a slightly worn body chamber steinkern from the drift (or Snettisham Clay?) near Hunstanton, Norfolk; photograph by Mr. B. J. Samuels. *c, d*, *Hoplocrioceras phillipsi* (Phillips), Yorkshire Museum, tablet 424 (Bean Collection), from the Speeton Clay of Speeton, Yorkshire. Photograph kindly given by Dr. M. K. Howarth, who photographically illustrated the specimen for the first time in this journal, vol. 5 for 1962. All photographs $\times 1$.

tubercles occur, sometimes common to two adjacent ribs, at other times limited to a single rib. Normally there are two non-tuberculate ribs between each of the tuberculate ones. The body chamber of B. 11797 has a very similar rib-pattern, but nearly every rib arises at the umbilical edge and most are single.

The suture-line is not adequately preserved on any of the specimens, but the septum has only four lobes, indicating a characteristic crioceratitid suture.

Genus HOPLOCRIOCERAS Spath, 1924
Hoplocrioceras phillipsi (Phillips)

Plate 43, figs. 7-8; text-figs. 1c-d, 2

- v* 1829 *Hamites phillipsi* (Bean MS.) Phillips, p. 124, pl. 1, fig. 30 (2nd edn. 1835; 3rd edn. 1875).
 v* 1924 *Hoplocrioceras phillipsi* (Phillips); Spath, p. 78.
 v* 1962 *Hoplocrioceras phillipsi* (Phillips); Howarth, p. 130, pl. 18, fig. 3.

Holotype. William Bean Collection, Yorkshire Museum, York, tablet 424.

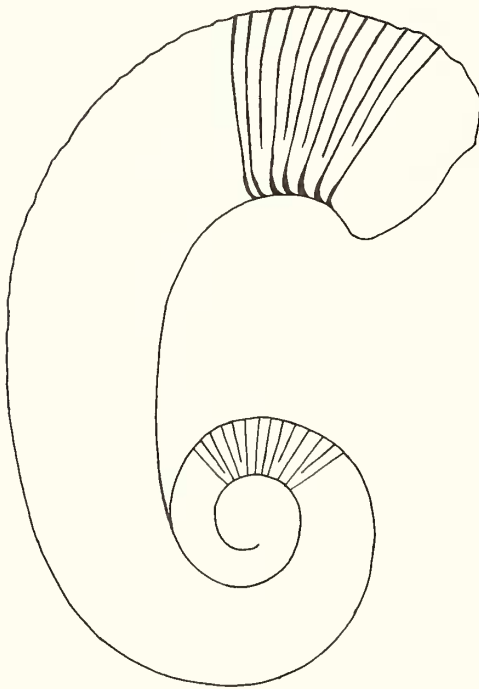
Type locality. Speeton, Filey Bay, Yorkshire.

Horizon. Speeton Clay. The exact horizon is not known, but the specimen is probably from the upper part of the Lower B Beds, of Lower Barremian age (see below).

Other material. One crozier: BM. C. 73594, from an unrecorded horizon in the Speeton Clay of Speeton.

Description. The holotype (text-fig. 1c-d) was described and refigured by Howarth (1962). It consists of about one and one-quarter septate whorls coiled so that the venter of one is just about in contact with the dorsum of the next, followed by a slightly crushed, incomplete body chamber which immediately (starting at 46 mm diameter) uncoils, though it remains slightly curved. The dorsum is not clearly visible, but the ventral region is rounded. The ribs are straight and single, with a few intercalated ribs appearing low on the whorl flank. Sutures are visible on the flanks and venter, and are clearly crioceratitid.

BM. C. 73594, the only other known example of the species, is a hooked body chamber (Pl. 43, figs. 7-8) with the last septum preserved. It represents a more advanced growth-stage than the holotype, but at a comparable stage the rib-pattern of both specimens is identical and the general shell proportions appear very similar when allowance is made for the slight crushing in the holotype. The dorsum is flat, crossed only by forwardly curving rib-folds and growth striae, the dorso-lateral edge slightly rounded and the ventro-lateral region well rounded, merging smoothly into the venter. The whorl section is almost elliptical, widest near the dorsum. The ribs are single and straight; primaries are raised slightly at the umbilical edge, exactly as on the body chamber of the holotype, and other ribs are intercalated low on the flank. On average, there is one intercalated rib between each primary, but the pattern is slightly irregular.



TEXT-FIG. 2. *Hoplocrioceras phillipsi* (Phillips). Reconstruction (based on the holotype and BM. C. 73594) to show the aspinoceratid mode of coiling, $\times 1$.

Discussion. Text-fig. 2 is a reconstruction of an adult *H. phillipsi* based on the two

specimens described here. The reconstruction supports Spath's (1924, p. 78) view that *H. phillipsi* is close to '*Ancyloceras laeviusculum* Koenen (1902, p. 350, pl. 28, figs. 4-6) with aspinoceratid coiling.

The horizon of *H. phillipsi* is not known, but the German *H. laeviusculum* came from the Lower Barremian *fissicostatum* Zone, the index species of which is known from Bed LB3 at Speeton (Rawson 1971, p. 72).

SPATH'S CONCEPT OF THE GENERA

Spath's definition of *Hoplocrioceras* and *Paracrioceras* was brief, and subsequent interpretation has necessarily relied mainly on some north German species, described by Koenen (1902) and earlier authors, which Spath (1924) also assigned to his new genera. These include forms very distinct from the type species. A full reappraisal of the scope of the genera must await a much-needed revision of the English and north German Barremian crioceratitid faunas; the following notes are limited to a discussion of Spath's concept of the genera in the light of his notes and faunal lists, coupled with the present revision of the type species.

Paracrioceras

No formal diagnosis was published, but Spath (1924, p. 84) noted that *Paracrioceras* is 'characterised by highly tuberculate ornamentation' and that it includes 'the Mediterranean *emerici* group', which resemble (p. 82) the *Paracrioceras* of the north German *roeveri* and *elegans* Zones. It also embraces (p. 85) the 'degenerate' forms of the *robustum* and *denckmanni* type. The faunal list from the Speeton Clay (pp. 77-78) and Snettisham Clay (p. 79) includes *P. statheri* Spath, *P. aff. varicosum* (Koenen), *P. aff. tuba* (Koenen), *P. aff. denckmanni* (Müller), *P. cf. woeckeneri* (Koenen), *P. cf. elegans* (Koenen), and the type species *P. occultum* (Seeley).

Some of the north German crioceratitids figured by Koenen (1902) have inner whorls close to those of *P. occultum* but with a body chamber ornamented only by well-spaced, strong, trituberculate ribs (e.g. *P. elegans*; Koenen 1902, pl. 24, fig. 2). The later forms which Spath regarded as 'degenerate' *Paracrioceras*, such as *P. denckmanni* (Müller), *P. stadlaenderi* (Müller), and *P. tuba* (Koenen), are more distinct from *P. occultum*. They are closely coiled with the whorls almost in contact, have strongly tuberculate inner whorls with few, widely spaced ribs, and by diameters of 65-70 mm have lost their tubercles and retain strong, distant, simple ribs only.

The earlier trituberculate whorls of *P. occultum* are very close to those of species of the Tethyan *emerici* group, which (as noted above) Spath also included in *Paracrioceras*. Sarkar's (1954) genus *Emericiceras* was proposed for these Tethyan forms and has been generally accepted by French authors (*Paracrioceras* being ignored), though it is often relegated to a subgenus of *Crioceratites* Leveille. *Emericiceras* is here regarded as a junior subjective synonym of *Paracrioceras*. In turn, *Paracrioceras* of the *occultum* group may be better regarded as a subgenus of *Crioceratites*. Typical *Crioceratites* of the *duvali* group differ from the trituberculate whorls of *P. occultum* only in having more numerous, finer, non-tuberculate ribs between the tuberculate ones, and in sometimes losing the mid-lateral tubercles. In both northern and southern Europe there is a gradation from *Crioceratites* of the *duvali* group in the

mid-Hauterivian to more coarsely trituberculate *Paracrioceras*/*Emericiceras* types in the Lower Barremian.

Wright (1957, p. L208) provisionally included *Hemicrioceras* Spath, 1924 (type species: *Crioceras rude* Koenen, 1902, from north Germany) and *Peltocrioceras* Spath, 1924 (type species: *Crioceras deecke* Favre, 1908, from Patagonia) in synonymy with *Paracrioceras*. The type species of both genera lack trituberculate ribs in the earlier growth stages and the genera should be kept distinct.

Hoplocrioceras

Again no formal diagnosis of the genus was published, but Spath (1924, p. 78) gave an idea of its intended scope by noting that the type species is 'a form close to *Crioceras laeviusculum* v. Koenen', while defining the genus 'to include also *Crioceras fissicostatum* (Roemer) Neum. & Uhlig, non v. Koenen?, and allied forms'. Thus he linked small aspinoceratid forms with larger species showing crioceratid coiling throughout growth. This was in agreement with his belief (p. 85) that the nature of the coiling is not of generic importance.

It is not absolutely clear what features Spath regarded as diagnostic of the genus. Subsequent authors (e.g. Anderson 1938; Wright 1957) have stressed the 'bundling of the ribs at the umbilical tubercle', though in its original context (Spath 1924, p. 84) this statement may have referred to the *fissicostatum* group only. Certainly neither *H. phillipsi* nor *H. laeviusculum* have bundled ribs or umbilical tubercles, though the ribs swell slightly at the umbilical edge on the body chamber. On the other hand, two factors indicate a close relationship between the two groups. Firstly, the specimen with bundled ribs on the outer whorl which Neumayr and Uhlig (1881, pl. 56, fig. 1) figured as *H. fissicostatum* (Roemer) can be matched by fragmentary individuals from the Speeton Clay in which the ribs in early growth stages are close to those of *H. phillipsi*. Secondly, *H. laeviusculum* occurs at the same horizon as members of the *fissicostatum* group in the north German Lower Barremian (Koenen 1902).

Some members of the *fissicostatum* group attain an adult growth stage in which the body chamber is ornamented only with strong, simple, tuberculate ribs; these include Koenen's (1902, pl. 22, figs. 1, 2) figured *H. fissicostatum*.

Aspinoceras Anderson, 1938 (type species *A. hamlini* Anderson) is here regarded as a junior subjective synonym of *Hoplocrioceras*. *A. hamlini* was based on a partly distorted specimen with non-tuberculate ribs 'often dividing near the dorsal border and on the upper part of the side' (Anderson 1938, p. 207). The illustrations suggest intercalation rather than division of the shorter ribs, and both rib pattern and coiling appear similar to *H. phillipsi*.

EXPLANATION OF PLATE 43

Figs. 1-6. *Paracrioceras occultum* (Seeley). Snettisham Clay, Heacham Brick Pit, Norfolk. Sedgwick Museum Collection, presented 1904. 1-3, SM. B. 11797; 4-6, SM. B. 11131. Figs. 1 and 6 are rubber casts from the natural external moulds visible on figs. 2 and 5; figs. 2-5 are natural moulds.

Figs. 7, 8. *Hoplocrioceras phillipsi* (Phillips). British Museum (Nat. Hist.) C. 73594 (pres. Dr. R. Francis, 1965). A crozier with shell preserved from the Speeton Clay of Speeton.

All photographs $\times 1$, by Mr. B. J. Samuels of Queen Mary College.



RAWSON, *Paracrioceras* and *Hoplocrioceras*

DISCUSSION: SHELL SHAPE, SUPRA-SPECIFIC CLASSIFICATION, AND DIMORPHISM

In most studies of the Hauterivian/Barremian heteromorphs of southern Europe, forms with ancyloceratid/aspinoceratid coiling are separated from crioceratid types at generic and subfamily level (e.g. Sarkar 1955; Thomel 1964; Wiedmann 1962). On the basis of their type species alone, *Paracrioceras* would thus be a typical member of the Crioceratitinae whereas *Hoplocrioceras* would be an early member of the Ancyloceratinae close to *Acrioceras*.

Spath's (1924) grouping of large crioceratid with smaller aspinoceratid forms in one genus (*Hoplocrioceras*) cuts completely across this procedure. An assessment of the relative merits of these differing schemes of classification is needed, but there is already some evidence to suggest that generic distinction on coiling alone may be unsound. Firstly, there are some other north-west European forms which show differing shell shapes but identical (and highly distinctive) sculpture. These are the species which Spath (1924) grouped into another new genus, *Parancyloceras*, of late Barremian age. The type species, *P. bidentatum* (Koenen), is one of several crioceratid species, but Spath also included in the same genus some small forms with initial coiled whorls and a straight shaft (with final hook?), such as *P. scalare* (Koenen). Both species groups have simple ribs which are often noticeably flattened on the venter and bear small ventro-lateral tubercles, and both occur at the same stratigraphical horizon.

Secondly, Thomel (1964) pointed out the remarkable similarity between the development and changes in sculpture of the Tethyan *Crioceratites* (subgenera *Crioceratites* and *Emericiceras*) and *Acrioceras* (subgenera *Acrioceras*, *Protacrioceras*, *Aspinoceras*, and *Paraspinoceras*) lineages. Referring to *Acrioceras* sensu lato, Thomel (1964, p. 72) noted 'this branch is incontestably connected to that of *C. duvali*. In fact, some species . . . show great similarities in ornamentation to *C. duvali* Lev., *C. nolani* (Kil.) and related forms from which they differ by their coiling. . . . The order of appearance of representatives of this race presents a curious parallelism with the succession of the sub-genera *Crioceratites* and *Emericiceras* in the course of the Hauterivian and Barremian' (author's translation from the French).

Thirdly, although all the species currently included in *Paracrioceras* are crioceratids, the type species is accompanied in the Snettisham Clay by body chambers of *Acrioceras* (recorded by Spath 1924 as *A. cf. tabarelli* Astier sp. and *A. cf. silesiacum* Uhlig sp.), one of which (SM. B. 11130) shows an impression of the inner whorls. These are very close to the comparable growth stage of *P. occultum*. This is exactly the relationship seen between *Emericiceras* (= *Paracrioceras*) and certain *Acrioceras* in the Tethyan faunas discussed above.

Thorough reassessment of the relative importance of coiling and sculpture in the supra-specific classification of these heteromorph forms must await more work on the stratigraphical distribution of the abundant Tethyan faunas. However, the evidence outlined here suggests that far from indicating differences that should be accommodated at subfamily level, the type of coiling may be unimportant even at generic level. The old idea that it may reflect sexual dimorphism is well worth examining in view of the increasing evidence that aspinoceratid/ancyloceratid forms occur at the same horizon as larger crioceratids with similar sculpture in the early whorls.

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PETER F. RAWSON
Department of Geology
Queen Mary College
Mile End Road
London E1

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